LIGHT THROWN BY THE EXPERIMENTAL STUDY OF HEREDITY UPON THE FACTORS AND METHODS OF EVOLUTION[1]

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THE most important contribution of modern studies in heredity to the topic of evolution has been *a new formulation of the problem.* Until a decade ago the problem of organic evolution was regarded as synonymous with that of the *origin of species.* We were, however, not agreed as to the definition of species; on the contrary, we realized that our notion of the term was exceedingly hazy. And, doubtless, the reason why we made so little progress in getting at the methods of evolution was because of this bad formulation.

To-day all this is changed. We think less of the origin of species and more of characteristics; of their nature, their origin and their distribution. The concrete question of the origin of a given species has become broken up into the questions of the origin of its differential *characters.* Thus, the problem of the origin of man has been broken up into the problems of loss of the tail, of the hairy coat, of skin pigmentation, of melanic iris pigmentation, the acquisition of a more complicated brain structure, the reduction of the lower part of the face, the acquisition of the ability to learn to count and talk, to wear clothes, to be honest, truthful, regardful of the property rights of others, and to exercise self-control in the sex sphere. So long as we formulated our problem as the explanation of the "origin of the human species," as though the human species were an indivisible unit, so

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long we floundered helplessly in the quicksand of unclearness and complexity; now that we recognize our study to be the history of any inheritable trait we move on surer ground. And so, in general, progress is to be made in the future by careful attention to the evolution of characters.

The second change in the formulation of the problem that is due to the modern study of heredity is that we no longer consider even the character as the ultimate unit of evolution, but regard it rather as a product of such a unit. For the character is, in some way or another, determined by the conditions in or the constitution of the germ-plasm and these conditions and this constitution, though very different from the adult characters, are their germinal representatives; and these germinal representatives are the real units to be studied. Thus we do not to-day formulate our problem as the evolution of man, or of a blue-eyed man, but ask how the determiner for brown-eye became lost from the germ-plasm. So, in general, the problem of evolution is formulated as that of the history of the germinal determiners of characters.

Besides formulating more precisely the problem of evolution, modern studies have discovered certain methods of evolution which were not appreciated a decade ago. First, we have come to realize that, though not uniformly, yet to a surprising degree, characteristics are *independent* of one another and, hence, that their determiners in the germ-plasm are commonly not bound together. The evidence for this is found in the breeding experiments that have been performed on scores of species of animals and plants, both feral and domesticated. Breeders have taken advantage of this independence to create almost any desired combination of known characters. Thus, in poultry the single pea or rose comb may be combined with a black, white or game plumage, with or without unfeathered shanks. The shepherd's purse that grows by the roadside may be made with either of two forms of capsules combined with

four forms of leaf in the rosette stage; fruit-flies (*Drosophila*) may have any one of several colors of eye combined with either short or long wings, and so on. The characteristics that are associated in an individual are, for the most part, not necessarily associated. The group of characteristics that distinguishes individuals of one "species" from those of another is largely an accidental one; and it is, therefore, not surprising that we so often find individuals which in one, two or several characters differ from the conventional description of their species, and these have in the past caused great difficulty to the species maker.

The fact that most characteristics are not necessarily associated—that they may occur in various combinations—certainly accounts for the multiplicity of "varieties" in domesticated species; and for much of the variation in feral species. Moreover, it probably accounts for the presence of many "species" in a genus. I may repeat here what I wrote in 1909.

Dr. Ezra Brainerd has shown how many wild "species" of *Viola* have arisen by hybridization, as may be proved by extracting from them combinations of characters that are found in the species that are undoubtedly ancestral to them. In such highly variable animals as *Helix nemoralis* and *Helix hortensis* it is very probable that individuals with dissimilar characters regularly mate in nature and transmit diverse combinations of characters to their progeny. Indeed, if one examines a table of species of a genus or of varieties of a species one is struck by the paucity of distinctive characters. The way in which species, as found in nature, are made up of different combinations of the same characters is illustrated by the following example, taken almost at random. Among the earwigs is the genus *Opisthocosmia,* of which the five species known from Sumatra alone may be considered. They differ, among other qualities, chiefly in the following characters (Bormans and Kraus, 1900):

Size: *A,* large; *a,* small.
Wing-scale: *B,* brown; *b,* yellow.
Antennal joints: *C,* unlike in color; *c,* uniform.
Forceps at base: *D,* separated; *d,* not separated.
Edge of forceps: *E,* toothed; *e,* not toothed.
Fourth and fifth abdominal segments: *F,* granular; *f,* not granular.

The combinations of these characters that are found are as follows:

Opisthocosmia	*ornata:*	*AbcDEF.*
	insignis:	*ABcDEf.*
	longipes:	*AbCDEf.*
	tenella:	*AbCdef.*
	minuscula:	*aBCDEf.*

Other species occur, in other countries, showing a different combination of characters, and there are characters not contained in this list, which is purposely reduced to a simple form; but the same principles apply generally.

The bearing upon evolution of the fact that species are varying combinations of relatively few characters is most important. Combined with the fact of hybridization it indicates that the main problem of evolution is that of the origin of specific characteristics. A character, once arisen in an individual, may become a part of any species with which that individual can hybridize. Given the successive origin of the characters *A, B, C, D, E, F,* in various individuals capable of intergenerating with the mass of the species, it is clear that such characters would in time become similarly combined on many individuals; and the similar individuals, taken together, would constitute a new species. The adjustment of the species would be perfected by the elimination of such combinations as were disadvantageous.

Second, modern studies have taught us that we have regarded the steps of progress in evolution in too crude a way. One school adhered to the view that characters, as we know them in the adult, arose gradually in phylogeny as in ontogeny, *i. e.,* that the germ-plasm undergoes a development as the child does. Another school proclaimed for discontinuity in phylogeny; *i. e.,* that the conditions in or the constitution of the germ-plasm undergoes from time to time more or less abrupt changes. Such abrupt changes are not altogether unknown in ontogeny; for the sundering of a chromosome or the perforation of a membrane involves essentially abrupt or discontinuous processes. The new era of experimental breeding is leading us to a position that is in some respects intermediate between the views of these two schools. We have discovered a hitherto unsuspected multiplicity of inheritable units, indicating a vaster complexity of the system of determiners in the germ-plasm

than we had dreamed. Sometimes a prominent character is represented by a single determiner like (perhaps) roseness of the comb of the fowl; but in most cases there is a multiplicity of factors, as in human hair and skin pigments, in the yellow of mice, in shank feathering of fowls and in seed coat-color of oats. In consequence of the fact of this multiplicity of factors and of the fact that a variable number may be present in different cases the adult character appears in numerous *grades* of development.

Indeed, the gradation of characters is, in these cases, such that one has to recognize that discontinuous variation passes over into continuous variation, in the sense that 40, 41, 42 form a continuous series, if not in the sense that x, $x + dx$, $x + 2dx$, etc., do. If a desire for uniformity leads us to conclude that all variations in the germ-plasm are discontinuous at least we see in many of these variations sufficient justification for the continuity hypothesis of the old-fashioned selectionist. The new light that has been thrown on the subject is the certainty of discontinuity in most cases and apparent continuity only in the limiting case. The reason why the old continuity hypothesis was for so long a time accepted was that we had underestimated the fineness and the multiplicity of the units of inheritance.

Third, experimental work has thrown a new light on the process of selection. It is clear that Darwin confused under this term two ideas that we now sharply separate; namely, the selection of the most favorable individuals and the selection of the most favorable blood, race, strain or pure line (biotype, Johannsen). In so far as not the soma but the germ-plasm is the proper basis of selection it is clear that the favorable biotype is what we should seek for to make most rapid advance. By this means Pearl has increased the fecundity of his poultry; thus, probably Castle has extended step by step the color pattern of rats; thus poultry fanciers have improved the color pattern of Barred Plymouth Rocks; thus I have gained a syndactyl race of fowl.

The method of personal selection has been widely used by the less philosophical breeders. I do not think it fair to Darwin to designate it as the exclusively Darwinian selection. Whether advance can be made by personal selection seems to me still an open question. Granting our inability to reason about genotypical constitution from the phænotypical, still, other things being equal, and in the long run and with great numbers of individuals an extremely high variant is more apt to belong to a genotype with a high mean than to one with a low or intermediate mean. Thus a breeder who selects merely the very best somas of a large number will be apt to select any superior biotype that may occur in his material. This is doubtless the reason why breeders who consider only the somas of their breeding stock nevertheless sometimes make progress; for they are occasionally fortunate enough to stumble upon a new biotype.

Fourth, the results of experiments have thrown light on the long-discussed question of the discontinuity between *species,* of the swamping effects of intercrossing new varieties with the parent species and the necessity for isolation to permit new varieties to become established as distinct species. We now realize that the danger of swamping which formerly seemed so logically necessary is, from our new point of view, not really to be seriously considered. Characters are rarely, if ever, swamped. Apparent swamping by intercrossing occurs when the new character depends on many determiners. But it is not, even in this case, really swamped; for no true blend occurs but, on the contrary, a segregation of the original extreme conditions takes place. This is well illustrated by the case of human skin color. When the germ cell that carries white skin color unites with the germ cell that carries black skin color the "white" character seems swamped in the offspring; but the swamping is only apparent. Two mulatto parents have children of various tints and, occasionally, one with a clear white skin, as well as one with a black skin like the original negro ancestor.

Neither white nor black is truly swamped. The extreme white or black conditions are rather rare, as is to be expected where a multiplicity of factors is involved. Thus, if there were two (2) factors P', P'' involved in the negro skin then in F_2 one in sixteen should be negro-black, one in sixteen pure white, and half of the remainder should be light mulatto and half dark mulatto. Although studies on this subject are not sufficient to warrant exact quantitative conclusions, it is certain that more than two and probably more than three factors are involved in the pigmentation of the negro. If a number of mulattoes inhabited (as sole occupants) an oceanic island, and bred there, in the course of generations both the white and the black types of skin color would be found again—the two extreme types are not swamped. Consequently from our present point of view, isolation is much less essential than was formerly thought to be the case. Practically important as it may be to keep races pure and ensure the absence of intergrades or hybrids, it is not essential to the survival of new traits that have arisen in the midst of the old stock.

Fifth, the experimental study of heredity has thrown light upon the question of the origin of *new determiners*. Every critical experiment that has been tried demonstrates again that the somatic condition exercises little or no influence upon the determiners in the germ-plasm. The first crucial experiment on this subject of which I know was that of Francis Galton, who infused into "silver-gray" does the blood of either yellow, black and white, or common agouti rabbits. In one case an angora buck and yellow doe had their carotid arteries so connected that for over half an hour the blood of each flowed into the body of the other; so that about one half of the blood of each was alienized. Yet, when the rabbits that had been operated upon were used as parents, the offspring indicated that their germ-cells had undergone no modification in consequence of the foreign blood. Recently the question has been revived by Guthrie, who

made the experiment of engrafting foreign ovaries into foster mothers very unlike the original females whence they were taken. He concluded that the offspring were modified in such a way as to prove that the transplanted germ-plasm had received something from the foster mother. Unfortunately Guthrie erred here, as my repetition of his experiments showed. For unquestionably, the hens that were operated upon regenerated their proper ovaries and produced no eggs from the engrafted ovaries. Dr. Phillips, working with Castle, engrafted black-bearing eggs from one female guinea pig into albino guinea pigs and then mated the females that had been operated upon with an albino male. All offspring were entirely black, proving, first, that the engrafted ovaries were functional and, second, that the determiners of the engrafted germ-plasm were not modified by the soma of the albino mother. On the other hand, the experiments of Standfuss, Tower and Kammerer on animals and MacDougal on plants apparently indicate that under the influence of various conditions of moisture, temperature and chemical action the *germ-plasm* may be changed. These results, probable as they are, await confirmation. If fully confirmed they will afford a picture of one way in which new determiners may originate.

Finally, some light has been thrown by modern experimental studies on the subject of *adaptation*—for Darwin the corner stone of organic evolution. But here, it must be confessed, the contribution has not been great. That there is such a thing as selective elimination is plainer than ever. That some characteristics are compatible with the environment and some incompatible is incontestibly true. Two cases in poultry illustrate this. I have a lot of rumpless fowl; the cocks are sexually active and the hens lay numerous eggs; but every egg is sterile, for the reason that the erection of the tail feathers in the hen is essential to the clean exposure of the cloacal opening for the transfer of the sperm. Hence, since in the rumpless hens the cloacal opening is not accessible to the

sperm, such a sport must, in nature, be eliminated. Under domestication it is continued by trimming away the feathers that cover the vent. Similarly, winglessness in male fowl renders copulation difficult because the wings serve the cock as balancers while treading the hen. These then are examples of characteristics that must be eliminated in nature. In the case of certain striking colors in poultry there is evidence that they are selected against; their possession gives their owner a handicap.

On the other hand certain new characteristics of fowl may be preserved because apparently they offer no handicap. Thus in the rumpless fowl the oil gland is absent and the birds seem to be none the worse on that account; their plumage is bright and quite as resistant to a wetting as that of birds with an oil gland at the base of the tail. The striking fact that our experimental work yields is the great number of new characters that seem to bear no relation to fitness or unfitness, but are truly neutral. Thus I can not find that polydactylism, shank-feathering or its absence, and the lower grades of single, pea and rose comb have any adaptive significance for poultry. One can invent adaptive explanations for them or their absence in birds, but there is no reason for thinking that the explanations are significant. On the other hand, there is accumulating considerable experimental support for Darwin's theory of sexual selection; but of this it is early to speak. On the whole, I think it may be fairly said that experimental work supports the principle of selective elimination but finds many characters that are wholly neutral.

To sum up, modern experimental study of heredity has given a new formulation to the problem of evolution and has given definite data on the method of evolution. It formulates the problem of evolution as the problem of the nature and origin of the germinal determiners of characters. It has shown that, for the most part, the new determiners arise one at a time and are independent of one another, may occur in any combination and may be

transferred from one strain or species to another. It has been shown that the unit characters are much more numerous and finer things than we had thought and, therefore, that the steps of evolution are frequently very small ones and are taking place in many directions. It has shown the relative unimportance of the isolation factor, since true blends of characters rarely, if ever, occur. It has demonstrated the lack of influence by soma upon germ-plasm; but has rendered it probable that external conditions may directly modify the determiners of the germ-plasm. It brings support for the view of selective elimination of undesirable traits but finds that many, if not most, characters that arise are neutral in respect to any adaptive significance. Finally, it looks forward with a justifiable expectancy to the completer experimental test of the factors of evolution and their eventual complete elucidation.

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